

TEMPORAL VARIATION IN THE REPRODUCTIVE CYCLE OF *MYTILUS EDULIS* L. (BIVALVIA, MYTILIDAE) FROM LOCALITIES ON THE EAST COAST OF THE UNITED STATES¹

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ABSTRACT

The reproductive condition of seven latitudinally separated populations of the mussel *Mytilus edulis* on the east coast of the United States was determined using histological analysis and stereology. Differences in the timing of various phases of the gametogenic cycle among populations did not have any discernible latitudinal trend. Two populations at the same latitude on Long Island, N. Y. had the greatest temporal differences observed in gametogenic cycle, with summer reproduction maxima separated by a 3-month interval. There was no difference in the water temperature regime between these two habitats and thus the rate of gametogenic development was not a constant function of temperature. The observed differences in the gametogenic cycle were attributed to temporal and quantitative differences between habitats in the energy content of the mussel's food supply.

INTRODUCTION

Marine benthic bivalves have a cyclical pattern of reproduction which can be divided into three phases: gametogenesis and vitellogenesis; spawning and fertilization; larval development and growth. Each species has a variety of adaptations, both genetic and nongenetic, which coordinate these reproductive events with the environment so as to maximize reproductive success. It has been well documented (for review see Sastry, 1979) that the duration of each stage of the cycle may be variable among species and the gametogenic cycle may either be annual, semianual, or continuous depending upon the species and environment. Although the reproductive cycles of numerous bivalve species have been described (reviewed by: Giese, 1959; Sastry, 1975, 1979; Seed, 1976; Andrews, 1979) there is still only partial understanding of the complex interactions between exogenous (*e.g.* food availability, temperature, salinity, *etc.*) and endogenous (nutrient reserves, hormonal cycle, genotype, *etc.*) variables that determine the initiation and duration of the various phases of the cycle, and thus ensure synchrony of gamete development within a population. This is of prime importance for dioecious species having external fertilization, which requires synchronized liberation of gametes.

Gametogenesis in *Mytilus edulis* is, in common with other boreo-temperate marine bivalves, a complex succession of events that eventually results in the for-

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Abbreviation: GVF, gamete volume fraction.

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mation of ripe gametes. Spawning is then followed by a period of reproductive recession and quiescence. Superimposed on the reproductive cycle is a nutrient storage cycle involving the accumulation of nutrients in the mantle which are mobilized for gametogenesis and for maintenance metabolism in the digestive gland (Gabbot, 1976).

In *M. edulis* which has a geographically broad distribution, in diverse habitats, the reproductive cycles of spatially separated populations differ (Seed, 1976). It is thus a suitable species in which to investigate the factors regulating the reproductive cycle by comparative studies of different populations.

This paper describes the reproductive cycles of two populations of *Mytilus edulis* on the north and south shores of Long Island, N. Y. We found such unexpectedly large differences in the gametogenic cycle of *M. edulis* between these two study sites that additional samples were collected from localities along the east coast of the United States in order to estimate the range of reproductive patterns found in geographically separated mussel populations. The documented differences in reproductive cycles will be related to certain environmental parameters in this report and to more detailed physiological cycles in subsequent publications.

MATERIALS AND METHODS

Animal collection

The two main study areas were located on the north shore of Long Island, New York, at Stony Brook and on the south shore, in Shinnecock Bay (Fig. 1). The Stony Brook population was situated between Mean Low Water Springs (M.L.W.S.) and mid-tide on a sheltered beach, at the confluence of Stony Brook Creek, which drains a tidal marsh, and Long Island Sound. The Shinnecock population was an intertidal mussel bed located between M.L.W.S. and mid-tide level in a lagoon, formed between Long Island and the Atlantic barrier beach. Animals, larger than 2.5 cm in shell length, were collected from both populations at approximately monthly intervals, between June 1976 and September 1979. On each sampling occasion salinity and temperature were recorded with a Beckman salinometer, and 10 l of seawater was collected and analyzed for total energy content, using the dichromate wet oxidation method (Newell, 1982).

The remaining five sampling areas were on the east coast of the United States (Fig. 1). Detailed environmental data are not available for these localities, but each was selected as being representative of a typical and viable eulittoral population of *Mytilus edulis* in that region. The only exception was the population from Narragansett Bay, which was approximately 0.3 m below mean low tide. Samples were taken from these populations only at intervals between April and October 1978, as indicated in Figure 1.

Measurement of reproductive condition

A piece of germinal tissue ($\approx 7 \times 4$ mm) was dissected from the same position in the gonad of each of 12 mussels. The tissue was fixed in Baker's formol calcium (+2.5% NaCl) for 24 h at 4°C prior to processing through an ascending alcohol series and embedding in paraffin wax. Two 7 μ m sections, cut from different depths within the block, were stained with haematoxylin and counterstained with eosin. The mussels' reproductive condition was assessed by stereology (Bayne *et al.*, 1978) and expressed as the "gamete volume fraction" (GVF), which is the proportion of the mantle tissue that is composed of follicles containing developing or ripe gametes.

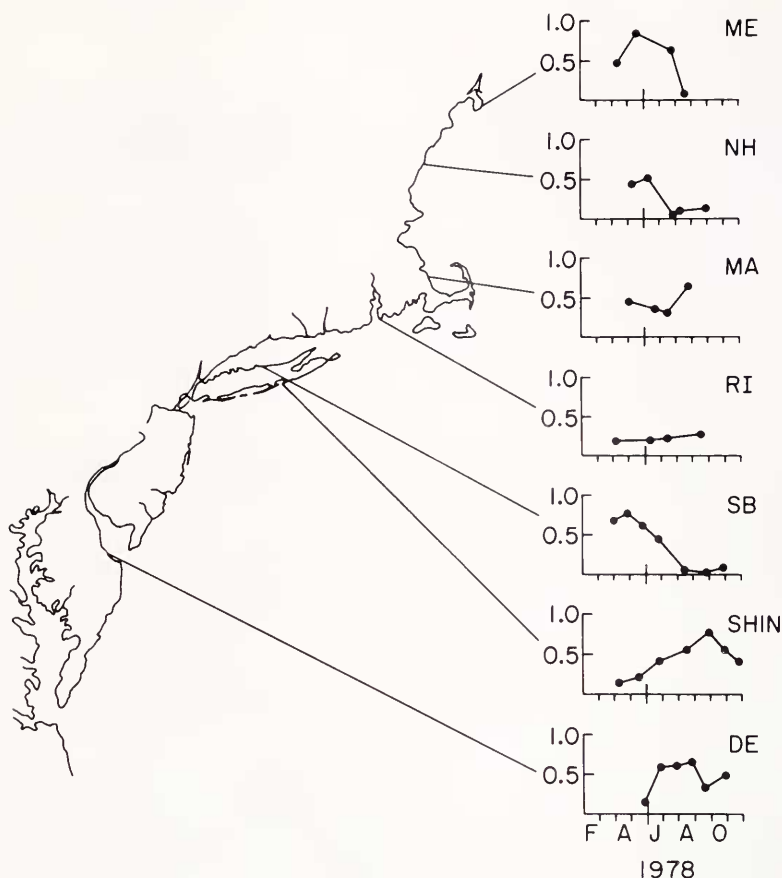


FIGURE 1. Mean reproductive condition for male and female *Mytilus edulis* from seven sites on the east coast of the United States. The reproductive condition, measured using stereology and expressed as Gamete Volume Fraction (G.V.F.) varies between 1.0 for a maximally ripe individual and 0.0 for an individual with no discernible gametes. Each point is a mean value calculated from 12 mussels (see text for further details). ME = Damariscotta River, Maine; NH = Newcastle, New Hampshire; MA = Cape Cod Canal, Massachusetts; RI = Narragansett Bay, Rhode Island; SB = Stony Brook, New York; SHIN = Shinnecock, New York; DE = Broadkill Inlet, Delaware.

Spaces within follicles which were observed when the mussels were maximally gravid were also counted in the GVF index. This was because the loss of gametes from these follicles probably only occurred either shortly before, or during the sampling process because the pressure from the rest of the gonad had not yet collapsed the intrafollicular space. The GVF can vary between zero, for a completely reproductively quiescent mussel, and one, for a mussel at peak reproductive condition. In this study, the mean of 10 estimates of the GVF of each animal (5 from each slide, cut from two different depths) was calculated and arcsine transformed (Sokal and Rohlf, 1969). Stereology is less subjective than the "index of bivalve gonad maturity" scheme proposed by Chipperfield (1953), where gonad squashes or stained sections are microscopically examined and assigned an arbitrary number (*c.f.*, Seed, 1976). Also, the Chipperfield technique does not fully recognize intermediate stages of development so the index results in nominal, rather than interval, measurements.

RESULTS

Long Island populations

The energy content of the seston at Stony Brook, expressed as joules per liter was consistently greater during the summer (May to October) than at Shinnecock (Fig. 2). During the remainder of the year there were sharp fluctuations in the energy content of the seston at both localities.

The mean salinity at Stony Brook was $24.2\text{‰} \pm 2.0\text{‰}$ (S.D.) and the temperature range was -0.5°C to 26.5°C (Fig. 3). Mean salinity ($29.1\text{‰} \pm 1.3\text{‰}$) was higher at Shinnecock, although the temperature range (Fig. 3) was very similar (0.8°C to 25.5°C) to that of Stony Brook. There is little tidal, and low annual, variation in salinity at these two localities (R.I.E. Newell, unpublished data), because neither area is associated with a river drainage system; most precipitation leaves Long Island by percolation through the sandy soil.

The reproductive condition (GVF) of male and female mussels from each population was analyzed separately to determine synchrony of their cycles. The mean GVF of each sex was compared using a Wilcoxon signed ranks test (Sokal and Rohlf, 1969) for all samples taken during a maturation phase (from the minima to maxima GVF) of the gametogenic cycles for each population; this tests the hypothesis that the same sexes mature at different rates within a population. In general, males had a higher GVF than did females during maturation; the difference was significant for the Shinnecock population ($P < 0.01$) but was not significant at Stony Brook ($P > 0.05$). Similar observations on the relative rates of reproductive maturation between sexes in the bivalves have been made for *M. edulis* (Seed, 1976) and *Cardium edule* (Newell and Bayne, 1980).

To facilitate comparisons of the average reproductive cycle of mussels from both populations, all male and female GVF valves were combined into a mean with 95% confidence limits for each sampling period (Fig. 4). Inspection of Figure 4 reveals that the reproductive cycle for *Mytilus edulis* at Stony Brook was constant between years in both the timing of the various phases of reproduction and the maximum reproductive condition attained. The post-spawning minimum GVF was in August/September, followed by a short period of reproductive quiescence from

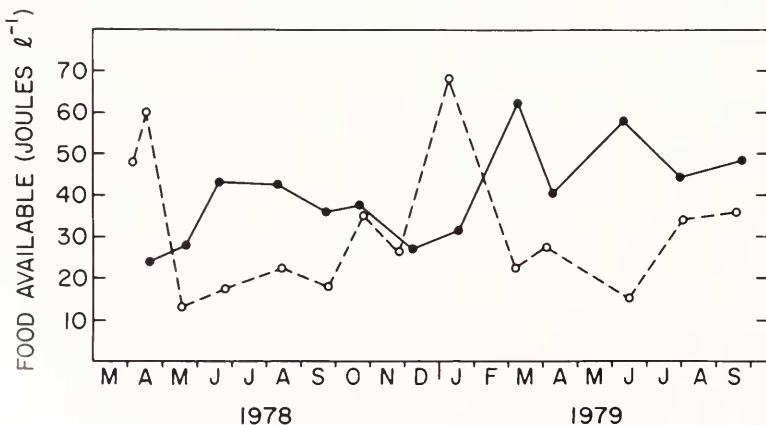


FIGURE 2. Seasonal changes in food availability (joules · l⁻¹) at Stony Brook (●—●) and Shinnecock (○- -○). Each point is the mean of 2 replicates.

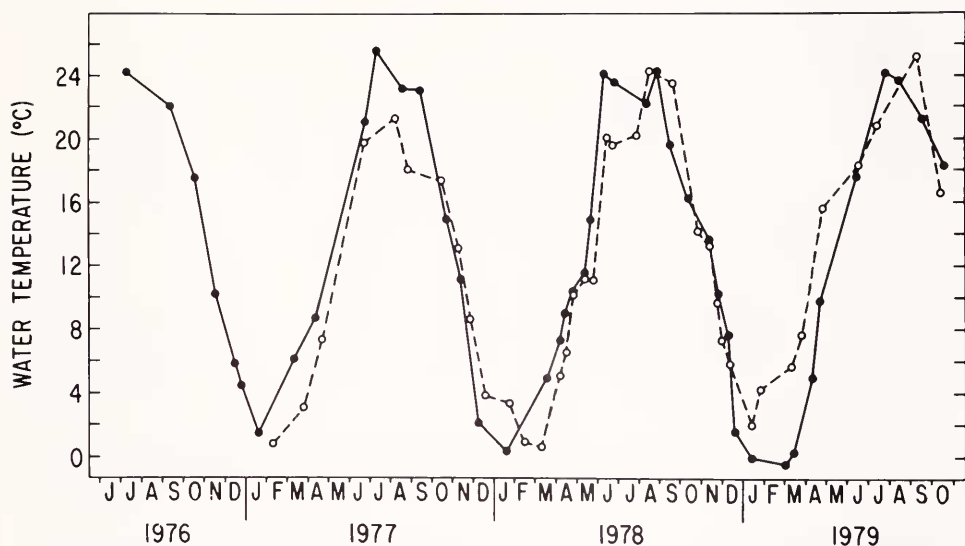


FIGURE 3. Seasonal variation in water temperature ($^{\circ}\text{C}$) at Stony Brook (\bullet — \bullet) and Shinnecock (\circ — \circ). Each point represents a single measurement of water temperature.

September to October. Gametogenesis was initiated again in November and continued through the winter, with a peak GVF of approximately 0.8 in April/May.

In contrast, the Shinnecock population appears to have a less regular cycle, with large between-year variation in both the timing of various phases of the gametogenic cycle and the annual maximum reproductive condition attained (Fig. 4). The maximum GVF varied from about 0.45 GVF (1977) to 0.8 GVF (1978), generally lower than at Stony Brook. In each year, maximum GVF occurred between July and October, or about three months later than at Stony Brook. Shinnecock animals exhibited a minimum GVF between March and May of approximately 0.12 to 0.25 compared to about a 0.05 GVF in September and October for Stony Brook mussels. The gradual decline in GVF during the autumn and winter in the Shinnecock mussels was probably not associated with the liberation of gametes by spawning, but rather due to their reabsorption by phagocytosis. Evidence in support of this was an increased number of haemocytes in the interfollicular tissue. The post-spawning quiescent period was maintained until about May in the Shinnecock mussel, which is considerably longer than in the Stony Brook population.

A more subtle difference between the two populations of *Mytilus edulis* was the degree of synchrony of maximum gametogenic condition among individuals within each population. In general, the variance in GVF estimated from the 12 mussels from each sampling period was greater in the Shinnecock population (Wilcoxon two sample test, $P < 0.001$) indicating a greater degree of intrapopulation synchrony in gametogenesis for the Stony Brook population. These differences are apparent when the mean and variance of GVF are illustrated together (Figs. 5 and 6). Stony Brook mussels were closely synchronized (*i.e.* lowest variance) during the entire period of gametogenesis, but as spawning proceeded individuals became asynchronous, indicating some variation in the time taken to liberate all gametes completely. The Shinnecock individuals were generally most asynchronous (*i.e.* highest variance) just prior to, and during, the period of maximum reproductive

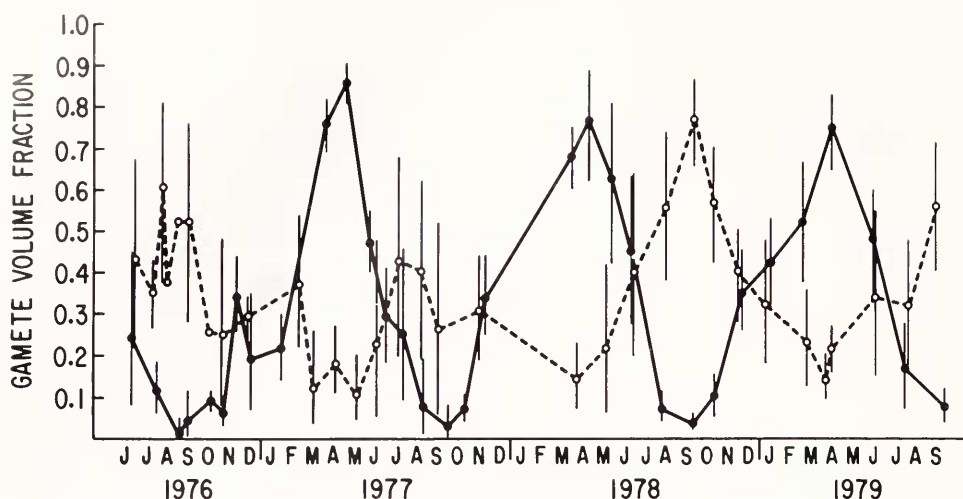


FIGURE 4. Mean reproductive condition (GVF) \pm 95% confidence limits for male and female *Mytilus edulis* combined from Stony Brook (● — ●) and Shinnecock (○ - - ○).

condition. This indicates that the Shinnecock mussel population was spawning over a protracted period.

In order to evaluate the dependence of gametogenic state upon an interaction of temperature and time, the number of cumulative degree-days were determined for each sample period by calculating areas under the curves in Figure 3 using a Spatial Data Systems (108 pt) image analyzer. The number of degree-days elapsed at each sample date since the GVF minima (ending with GVF maxima) was estimated. Since cumulative degree-days were calculated starting with the annual minima in GVF, this analysis dictates a positive regression of GVF on elapsed degree-days; the comparison of interest is in the slopes of these regressions. If the gametogenic state of the two populations is largely dependent upon elapsed degree-

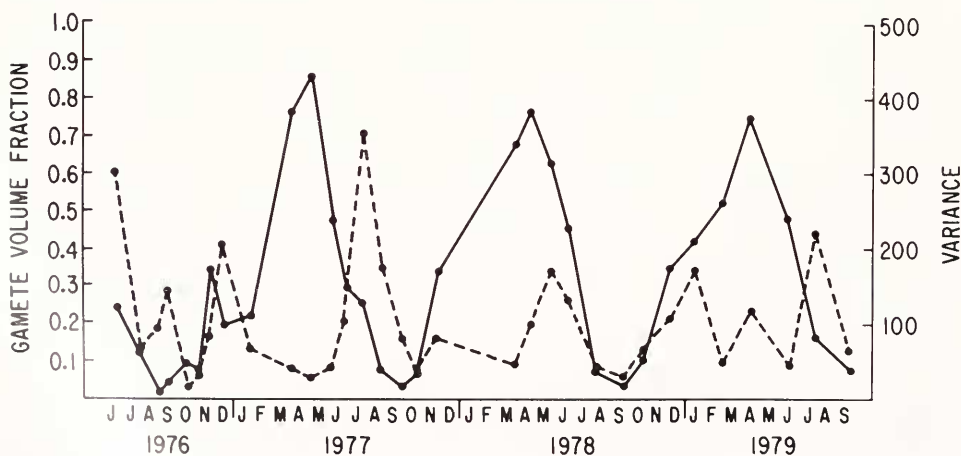


FIGURE 5. Mean reproductive condition (GVF; ● — ●) and variance (● - - ●) for male and female *Mytilus edulis* from Stony Brook.

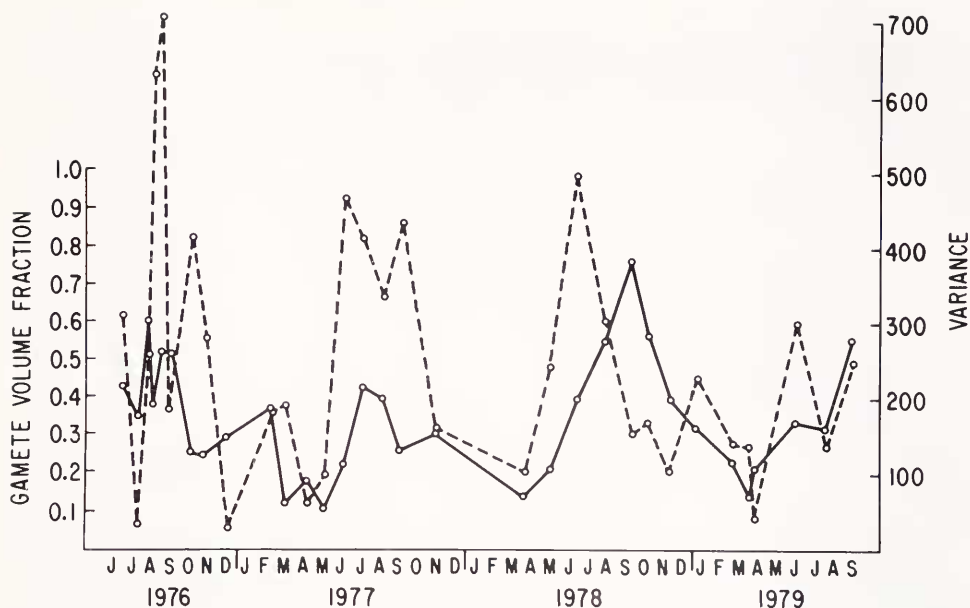


FIGURE 6. Mean reproductive condition (GVF; ○—○) and variance (○- - -○) for male and female *Mytilus edulis* from Shinnecock.

days, the slopes will be similar. Analysis of covariance revealed heterogeneous slopes when all four regression lines were compared ($F_{\{3,9\}} = 10.25$; $P < 0.005$; Fig. 7). A simultaneous test procedure (Sokal and Rohlf, 1969) demonstrated that within population regressions between years had similar slopes while the slopes between populations were clearly different. This analysis suggests that differences in gametogenic cycles between the Stony Brook and Shinnecock populations were not directly related to any difference in schedule of degree-days (*i.e.* temperature).

N.E. coast populations

The mean reproductive condition of combined males and females from seven localities (including Stony Brook and Shinnecock) along the N.E. Atlantic Coast demonstrates large variation in the timing of maximum GVF (Fig. 1). This ranged from a peak in reproductive condition in May (Maine) to a peak in September (Shinnecock). The Rhode Island population had no obvious reproductive maxima during the six summer months. The differences between Stony Brook and Shinnecock, described earlier, were greater than between any other two sampled localities. There was no clear latitudinal trend in the timing of maximum GVF.

DISCUSSION

There have been many attempts to determine the key environmental factor(s) that synchronize the reproductive cycle among individuals within marine invertebrate populations to prevailing environmental conditions. Water temperature, which varies with season and latitude in a moderately uniform manner, frequently has been assigned a dominant synchronizing role. It has been found for certain species that the reproductive cycles of latitudinally separated populations were predictably different (Orton, 1920; Thorson, 1946). Thus a northern hemisphere boreal-tem-

a threshold temperature, or possibly a rate of change in temperature (Chipperfield, 1953; Bayne, 1975), is a very important factor influencing gametogenesis and acting as a trigger for spawning. However, gamete production is ultimately dependent on the nutrients available for gametogenesis, either in terms of a nutrient reserve or food recently ingested.

Mytilus edulis is normally dependent on a nutrient reserve, accumulated during the immediate post-spawning period (Gabbot, 1976) when food is abundant, to provide energy for gametogenesis and catabolism during the winter. Spawning then is usually timed such that both larvae and adults have access to abundant supplies of food; this maximizes the probability of successful recruitment and the rate of energy acquisition by adults for the following reproductive season (Bayne, 1976; Sastry, 1979). It is evident that environmental variation between habitats resulting in altered availability of food or the individual's capacity to assimilate nutrients will alter the nutrient storage cycle and the timing of gametogenic events.

There were distinct differences in both the amount and seasonal availability of energy to the Stony Brook and Shinnecock populations (Fig. 2). At Stony Brook food is most abundant in the late spring and summer, when mussel feeding rates are at a maximum, leading to the occurrence of maximal assimilation rates (R.I.E. Newell, unpublished data). Mussels at Stony Brook spawn in April/May just prior to, or during, the period of maximum food availability (Fig. 2). They can obtain sufficient nutrients from the seston during this post-spawning period to accumulate a food reserve as is considered typical for the species (Gabbott, 1976). In contrast, the Shinnecock population faces low levels of energy in the seston and unpredictable and sharp temporal peaks in energy availability during the same time of the year. The maximum seston energy levels were recorded during the winter when feeding rates are depressed (R.I.E. Newell, unpublished data). These factors lead to reduced total assimilation. Thus the high degree of synchrony in maximum gametogenic condition (and cyclicity) within the Stony Brook population reflects the timing and temporal variation in local food availability and of the long period during the winter in which gametogenesis may proceed. In the Shinnecock population, because maximum food availability occurs when the animals are not actively feeding, there is no period of maximum energy assimilation to give rise to a nutrient storage cycle. Instead, two possibilities exist: (1) individuals may initiate a "typical" gametogenic cycle once sufficient nutrient reserves are accumulated, but if environmental cues are lacking, individuals in the population are not synchronized, or (2) individuals develop gametes and hence spawn piecemeal as soon as sufficient reserves are gathered. Both of these conditions constitute "dribble spawning" with respect to the population.

Annual differences in maximum reproductive condition and fecundity have been previously noted in a *M. edulis* population by Thompson (1979) who attributed the differences to annual variations in the food supply in coastal inlets of Nova Scotia. He also found no differences in fecundity between 1974 and 1975 in the Stony Brook population, which supports our observation of a very constant maximum gamete volume fraction over the three year study period.

Griffiths (1977) found that in South African populations of *Choromytilus meridionalis*, which do not accumulate large nutrient reserves, the quantity of gametes released varied annually. Griffiths (1977) concluded that "food availability may be of greater importance in maturation of the gonad than temperature". This supports the argument propounded by Bayne (1976) that gametogenesis in some species is buffered from environmental change by a nutrient reserve. In other more

"opportunistic" species, gametogenesis is more closely linked to the current food supply which allows them to capitalize on particularly favorable environmental conditions, e.g., high phytoplankton production. However, the results of our study indicate that there may not be such a single reproductive "strategy" for a species but rather a variety of different patterns, depending on the particular environmental regime.

It is interesting to speculate on the adaptative significance of a peaked spring spawning period, compared to an extended one for planktotrophic mollusc species when similar numbers of gametes are liberated (Todd and Doyle, 1981). In the former case there is a highly probability of fertilization of the egg (Sastry, 1979). Also, larvae may be produced at the most opportune moment with regard to food availability (Sastry, 1975) and still have sufficient time both to outgrow predation rapidly (Seed and Brown, 1978) and accumulate a nutrient reserve before the onset of winter. In the latter case there is continuous dribble spawning, and hence prolonged recruitment, which means that in the event of a catastrophe in an unpredictable environment, which could kill or prevent settlement of the vulnerable larvae, only a portion of the potential recruits would be lost. Our data suggest that for sessile invertebrates neither pattern may necessarily be adaptative but may simply be a manifestation of variation in exogenous factors.

The temporal differences in the reproductive cycles of adjacent *M. edulis* populations recorded in this study have also been noted for the species by Moore and Reisch (1969) within Alamitos Bay, California. However, the environmental cause of these differences could not be determined. Also, Wilson and Hodgkin (1967) concluded that although temperature probably controlled the overall reproductive cycle (i.e. duration and season of gametogenic activity) in five species of mytilids on the western Australian coast, some unknown factor regulated the finer detail of the cycle (i.e. the intensity and duration of spawning and exactly when it occurred).

Bayne (1975) in a comprehensive review of reproduction in *M. edulis* concluded that both "temperature and the food level serve to synchronize different stages in the gametogenic cycle." Blake and Sastry (1979) found that temperature and nutrient availability interact with neurosecretory cycles of *Argopecten irradians* in a complex manner to control the initiation of gametogenesis. The nature of these interactions changed as the reproductive cycle proceeded. Similarly Sastry (1970) found that a population of *Argopecten irradians* from North Carolina reached its reproductive peak 3 months after a population from Massachusetts. This conflicts with the simple latitude/temperature zoogeographic principle discussed previously. Sastry (1970) suggested that the differences might be "an adaptative response to geographical differences in the period of abundant food production and temperatures."

Thus, superimposed on the overall affect of latitude (and hence by implication, water temperature) on the reproductive cycle of bivalves must be variations due to habitat-specific differences in the time and duration of maximum food availability. The animals' physiological adaptations must also be considered as they can potentially be adjusted to maximize the animals' fecundity and hence competitive ability in a particular environment.

Geographic variation in reproductive cycle, whatever the cause, has also been attributed to the existence of "physiological races" (Loosanoff and Nomejko, 1951), implying genetic differences among populations. Populations of *M. edulis* along the Atlantic coast of North America are known to be genetically differentiated (Koehn

et al., 1976; Koehn *et al.*, 1980), and the relationship between genetic differences and variation in the physiology of reproduction will be considered in a subsequent paper.

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